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Ancient genome-wide analyses infer kinship structure in an Early Medieval Alemannic graveyard

O'Sullivan, Niall ; Posth, Cosimo ; Coia, Valentina ; Schuenemann, Verena J ; Price, T. Douglas ; Wahl, Joachim ; Pinhasi, Ron ; Zink, Albert ; Krause, Johannes ; Maixner, Frank

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ANTHROPOLOGY

Ancient genome-wide analyses infer kinship structure in an Early Medieval Alemannic graveyard

Niall O'Sullivan^{1,2,3*}, Cosimo Posth^{2,4}, Valentina Coia¹, Verena J. Schuenemann^{4,5†}, T. Douglas Price⁶, Joachim Wahl^{7,8}, Ron Pinhasi^{3,9}, Albert Zink^{1*}, Johannes Krause^{2,4*}, Frank Maixner^{1*}

From historical and archeological records, it is posited that the European medieval household was a combination of close relatives and recruits. However, this kinship structure has not yet been directly tested at a genomic level on medieval burials. The early 7th century CE burial at Niederstotzingen, discovered in 1962, is the most complete and richest example of Alemannic funerary practice in Germany. Excavations found 13 individuals who were buried with an array of inscribed bridle gear, jewelry, armor, and swords. These artifacts support the view that the individuals had contact with France, northern Italy, and Byzantium. This study analyzed genome-wide sequences recovered from the remains, in tandem with analysis of the archeological context, to reconstruct kinship and the extent of outside contact. Eleven individuals had sufficient DNA preservation to genetically sex them as male and identify nine unique mitochondrial haplotypes and two distinct Y chromosome lineages. Genome-wide analyses were performed on eight individuals to estimate genetic affiliation to modern west Eurasians and genetic kinship at the burial. Five individuals were direct relatives. Three other individuals were not detectably related; two of these showed genomic affinity to southern Europeans. The genetic makeup of the individuals shares no observable pattern with their orientation in the burial or the cultural association of their grave goods, with the five related individuals buried with grave goods associated with three diverse cultural origins. These findings support the idea that not only were kinship and fellowship held in equal regard: Diverse cultural appropriation was practiced among closely related individuals as well.

INTRODUCTION

The Alemanni were a confederation of Germanic tribes that inhabited the eastern Upper Rhine basin and surrounding region (Fig. 1) (1). Roman ethnographers mentioned the Alemanni, but historical records from the 3rd to the 6th century CE contain no regular description of these tribes (2). The upheaval that occurred during the European Migration Period (*Völkerwanderung*) partly explains the interchangeability of nomenclature with the contemporaneous Suebi people of the same region and periods of geographic discontinuity in the historical record (3). This diverse nomenclature reflects centuries of interactions between Romans and other Germanic groups such as the Franks, Burgundians, Thuringians, Saxons, and Bavarians. With the defeat of the Alemanni by Clovis I of the Franks in 497 CE, Alamannia became a subsumed Duchy of the Merovingian Kingdom. This event solidified the naming of the inhabitants of this region as Alemanni (3). From the 5th to the 8th century CE, integration between the Franks and the Alemanni was reflected by changed burial practices, with households (*familia*) buried in richly furnished graves (*Adelsgrablege*) (4). The splendor of these *Adelsgräber* served to demon-

strate the kinship structure, wealth, and status of the *familia* and also the power of the Franks (*Personenverbandstaaten*, a system of power based on personal relations rather than fixed territory). Because inclusion in *familia* during the Merovingian period was not necessarily based on inheritance or provenance, debate continues on the symbolism of these burial rites (5).

The 7th century CE Alemannic burial site at Niederstotzingen in southern Germany, used circa 580 to 630 CE, represents the best-preserved example of such an Alemannic *Adelsgrablege*. Discovered in 1962 (Fig. 1) (6, 7), 13 human skeletal remains (10 adults and 3 infants), along with a varied assemblage of weapons, armor, jewelry, equestrian gear, and remains of three horses, were excavated from 12 graves. The grave goods indicated contacts with Byzantines, Lombards, and Franks (Table 1 and fig. S1). These outside contacts appear to have been facilitated by equestrianism and guardianship of a nearby Roman crossroads. Two of the 12 graves (3 and 12) were multiple burials containing three individuals each, from which it has been inferred that they had close familial relationships (8). Both multiple burials contained Byzantine artifacts, lamella helmet (grave 12, individual 12B), and equestrian gear with Byzantine engravings (grave 3, individual 3A), suggesting eastern Mediterranean contact, whereas those buried with Frankish (individual 9) and Lombard (individual 6) artifacts support contact with eastern France and northern Italy (6, 8, 9).

Since the initial discovery of Niederstotzingen, bioarcheological analyses have provided additional information from the remains (section S2). Strontium and oxygen isotope data from the enamel showed that most individuals are local rather than migrants (Table 1, table S2, and fig. S2), except for individuals 10 and 3B. Polymerase chain reaction (PCR)-based sex estimation and reconstruction of the mitochondrial DNA (mtDNA) hypervariable region offered the first genetic characterization of the individuals (table S1) (8). Despite these findings, there are still questions regarding

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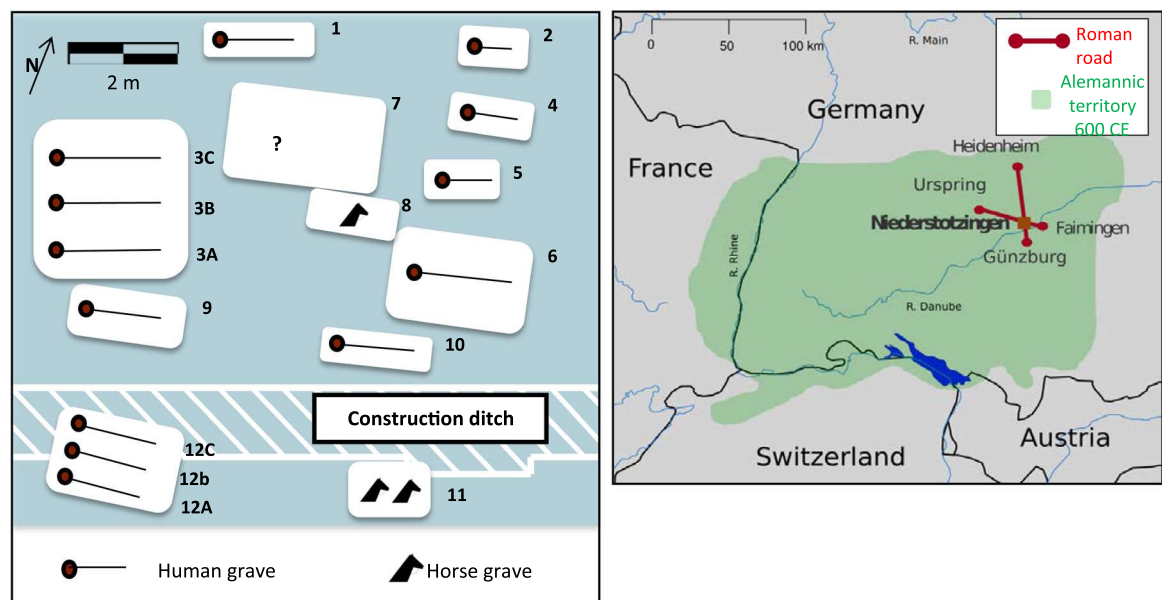


Fig. 1. Burial site reconstructions and location. (Left) Burial orientation of human and horse graves at Niederstotzingen. **(Right)** Location of burial site in southwest Germany.

Table 1. Archeological context, karyotype sex estimates, haplotypes, contamination estimates, and isotopic data from Niederstotzingen. Strontium values that indicate provenance outside of the region. Full list of mtDNA and NRY haplotypes is given in tables S8 and S9. Complete summary of contamination estimates for mitochondrial and X chromosome on 1240K capture and SE is given in tables S6 and S7. Genetic sex estimates are based on shotgun and 1240K capture. Individuals highlighted in red and green are from two multiple burials, graves 3 and 12 (Fig.1).

Individual	Archeological context	Age at death estimate (years)	Genetic sex	MtDNA/NRY haplotype	Median mtDNA/X (SE) contamination	Strontium ⁸⁷ Sr/ ⁸⁶ Sr
1	—	40–50	Male	K1a/R1b1a2a1a1c2b2b1a1	0.03/0.002 (0.003)	0.7089
2	—	9–11	Male? *†	K1a1b2a1a/-	0.15/—	0.7093
3a	Byzantine	20–30	Male	K1a/R1b1a2a1a1c2b2b1a1	0.02/0.0145 (0.007)	0.709
3b	—	50–60	Male	I5a1b/G2a2b1	0.03/0.0009 (0.0024)	0.7104†
3c	—	20–30	Male	T2/R1b1a2	0.03/0.0404 (0.0203)	0.7089
4	—	2	Male	X2b4/-	0.03/—	0.7094
5	—	0.5–2	Male? *†	K1a1b2a1a/-	0.04/—	0.7096
6	Lombardian	14–17	Male	H65a/R1b1a2a1a1c2b2b	0.02/–0.0007 (0.00117)	0.7093
9	Franconian	40–50	Male	X2b4/ R1b1a2a1a1c2b2b1a1	0.04/–0.0047 (0.00466)	0.7089
10	—	20–25	Male*	H1b/R1	0.06/—	0.7105†
12a	—	25–35	Male*	H10e1/R1b1	0.09/—	0.7087
12b	Byzantine	30–40	Male	X2b4/ R1b1a2a1a1c2b2b1a1	0.03/0.0128 (0.0136)	0.709
12c	—	20–30	Male	U5a1a1/ R1b1a2a1a1c2b2b1a1	0.03/0.0010 (0.0078)	0.7093

*Statistically insignificant sex estimate but consistent with maleness (table S10 and fig. S4). †After PMD filtering, individuals 2 and 5 had insufficient reads for accurate sex estimation (table S13).

their genetic sex, kinship, and genetic origin, because of the technical challenges of ancient DNA (aDNA) analysis (10). Typically, DNA extracted from archeological remains contains only trace amounts of endogenous human DNA. Furthermore, multiple waves of migration and recent admixture can make it challenging to genetically distinguish ancient populations inhabiting nearby geographical locations (11, 12). Single-nucleotide polymorphisms (SNP) in recombining regions of autosomes and the X chromosome are especially

useful for analysis of population affiliations (13, 14) and kinship (15, 16). These SNPs contain ancestral information from a large number of an individual's ancestors, unlike the nonrecombining maternally inherited mtDNA and paternally inherited Y chromosome each representing only an ancestral lineage.

To increase the resolution of kinship and population genetic analysis, we analyzed the individuals recovered from Niederstotzingen by using an approach that combined targeted DNA enrichment of more than 1 million SNPs (17) with high-throughput sequencing. Through joint analysis of mtDNA, Y chromosome [the nonrecombining region (NRY)], and autosomal SNPs, we aimed to reconstruct potential familial relationships of the Niederstotzingen individuals and estimate their genetic sex. In combination with archeological and isotopic data, we directly tested historical and archeological hypotheses positing that Alemannic burial practices, through assortment of deceased individuals and their associated artifacts, are a reflection of mobility and kinship structure. Our results provide insight into the medieval household (*familia*) and the role of multiple burials at Niederstotzingen. Previous studies have shown that the genetic affiliations of ancient people often do not match putative geographic origin of their culture (5, 18). Hence, we investigated the congruence between the biological provenance and the cultural origin of burial rites and goods present at Niederstotzingen. Our results shed new light on the kinship structure in Early Medieval Europe and investigate whether contacts at Niederstotzingen to southern Europe and elsewhere went beyond the exchange of material artifacts. The results show that 11 of the individuals are likely males, suggesting a sex-biased burial practice, 5 of whom are detectably related to at least second degree. These five related individuals had culturally diverse grave goods despite the evidence that all of them showed local isotope signals with northern European genetic affiliations; these data show how diverse cultural appropriation could exist even among close relatives.

RESULTS

Authentication of sequenced data

To assess the quantity and quality of the extracted DNA, we performed shotgun sequencing before capture and mapped the sequences to the human genome. The percentage of endogenous DNA varied considerably between sequenced samples (<1 to 75%), showing different rates of endogenous DNA preservation among individuals and even in subsamplings from the same individual (table S3). Captured libraries showed increased percentage abundance mapping at target loci compared to shotgun libraries: between 273- and 2494-fold target enrichment efficiency for mtDNA and between 22- and 232-fold target enrichment efficiency for the 1240K SNP capture (tables S4 and S5). Deamination patterns at the 5' and 3' ends, typical of aDNA damage in non-UDG (uracil-DNA glycosylase)-treated libraries (fig. S3), indicate that there are endogenous sequences present. Low contamination estimates of the uniparental markers obtained with the software Schmutzi on mtDNA and ANGSD (analysis of next-generation sequencing data) on the X chromosome further support the authenticity of our ancient human DNA (Table 1 and tables S6 and S7). Exceptions were individuals 2, 10, and 12A that had a median mtDNA contamination above 5%. For these mitogenomes, low-covered and ambiguous mtDNA positions were further stringently filtered through visual inspection with Integrative Genomics Viewer (19) and compared with PMDtools filtered reads.

Analysis of uniparental markers

mtDNA haplogroups were successfully assigned to all 13 individuals (Table 1). Notably, there are three groups of individuals that share, among the assigned positions, identical haplotypes: individuals 4, 9, and 12B in haplogroup X2b4; individuals 1 and 3A in haplogroup K1a; and individuals 2 and 5 in haplogroup K1a1b2a1a (table S8). Postmortem deamination (PMD) PMDtools filtering (threshold 3) of mtcapture sequences of individuals 2, 10, and 12A (that showed contamination estimates greater than 5%) did not change the main haplogroup; only 12A's haplogroup becomes less derived (table S14).

Despite low coverage across the Y chromosome in the 1240K, the NRY haplogroups of 10 individuals were successfully recovered (Table 1 and tables S3 and S9). Most individuals belong to the R1b haplogroup (individuals 1, 3A, 3C, 6, 9, 12A, 12B, and 12C), which has the highest frequency (>70%) in modern western European populations (20). Five individuals (1, 3A, 9, 12B, and 12C) share the same marker (Z319) defining haplogroup R1b1a2a1a1c2b2b1a1. Because of incomplete SNP capture and coverage on the Y chromosome, most of the individual's haplotypes do not overlap across the entire International Society of Genetic Genealogy (ISOGG) Y-haplogroup tree, but multiple positions with the same haplotype and/or consistent root allow estimation of Y chromosome ancestry anyway. For example, individuals 1, 3A, and 6 have R1b lineage and marker Z347 (R1b1a2a1a1c2b2b), which belongs to the same male ancestral lineage as marker Z319. Individual 3B instead carries NRY haplogroup G2a2b1, which is rare in modern north, west, and east European populations (<5%), only reaching common abundance in the Caucasus (>70%), southern Europe, and the Near East (10 to 15%) (21).

Sex determination of individuals

Genetic-based sex estimates, using shotgun and 1240K capture data, show that at least 11 of the individuals were probably male. From shotgun sequences, 1, 3A, 3B, 3C, 4, 6, 9, 12B, and 12C have statistically significant rates of male DNA, while 2, 5, 10, and 12A are low-covered but consistent with the presence of male DNA (Table 1 and table S10). To further validate authenticity of these data, shotgun sequences were filtered for reads with PMD with PMDtools (threshold 3) (22). Sex estimates were largely consistent for filtered data, except 3A, 3C, and 12B, which lost statistical significance, and individuals 2 and 5, which had insufficient reads remaining (table S13). The normalized ratio of X chromosome to autosomal reads provided a robust estimate of sex for shotgun libraries that had extremely low coverage, except for individuals 5 and 12a (table S11) (23). The ratio of captured X and Y chromosome SNPs to autosomal SNPs in the 1240K also shows a similar proportion of X and Y SNPs, further supporting the indication that all the individuals are males (fig. S4 and table S10) (24).

Genotyping and population affinity of genome-wide capture

After 1240K capture, between 29,673 and 374,347 called SNPs overlapped with the Human Origins Database (25, 26), providing enough genomic markers for accurate estimates of genetic affinity (1, 3A, 3B, 3C, 6, 9, 12B, and 12C) (Table 1 and table S5). The projections of the ancient genomic data on principal components analysis (PCA) built with modern west Eurasians show that six individuals from Niederstotzingen (1, 3A, 6, 9, 12B, and 12C, hereafter referred to as Niederstotzingen North) have the greatest affinity with modern

northern, eastern, and central Europeans, while individuals 3B and 3C (hereafter referred to as Niederstotzingen South) have the greatest affinity with southern Europeans and individuals from the eastern Mediterranean (Fig. 2). Admixture analysis with five components that had the optimum cross-validation (CV) error (table S12) indicates that Niederstotzingen North individuals have the most similar admixture components to modern-day eastern European populations (fig. S5). Niederstotzingen South individuals have a proportion of components that most resemble modern Mediterranean populations. However, 3B and 3C do not have similar proportions of ancestry to one another unlike Niederstotzingen North individuals.

To formally test the extent of shared genetic drift among individuals, outgroup F3 statistics were applied to the autosomal data using populations guided by PCA projections. F3 statistics (Mbuti;

Niederstotzingen individual, modern west Eurasian) concur with PCA and admixture estimates, showing that Niederstotzingen North individuals are closely related to northern and eastern European populations, particularly from Lithuania and Iceland. Niederstotzingen South individuals have the greatest affinity to southern Europeans (figs. S6 to S13), in particular to populations from modern northern Spain, but have a much weaker population affinity to any European population overall, thus suggesting recent admixture between different populations in their ancestry.

Estimation of kinship

To investigate kinship between the individuals, we made pairwise estimates of first- and second-degree kinship based on the proportion of nonmatching autosomal genotypes (P0) in each unique pair from

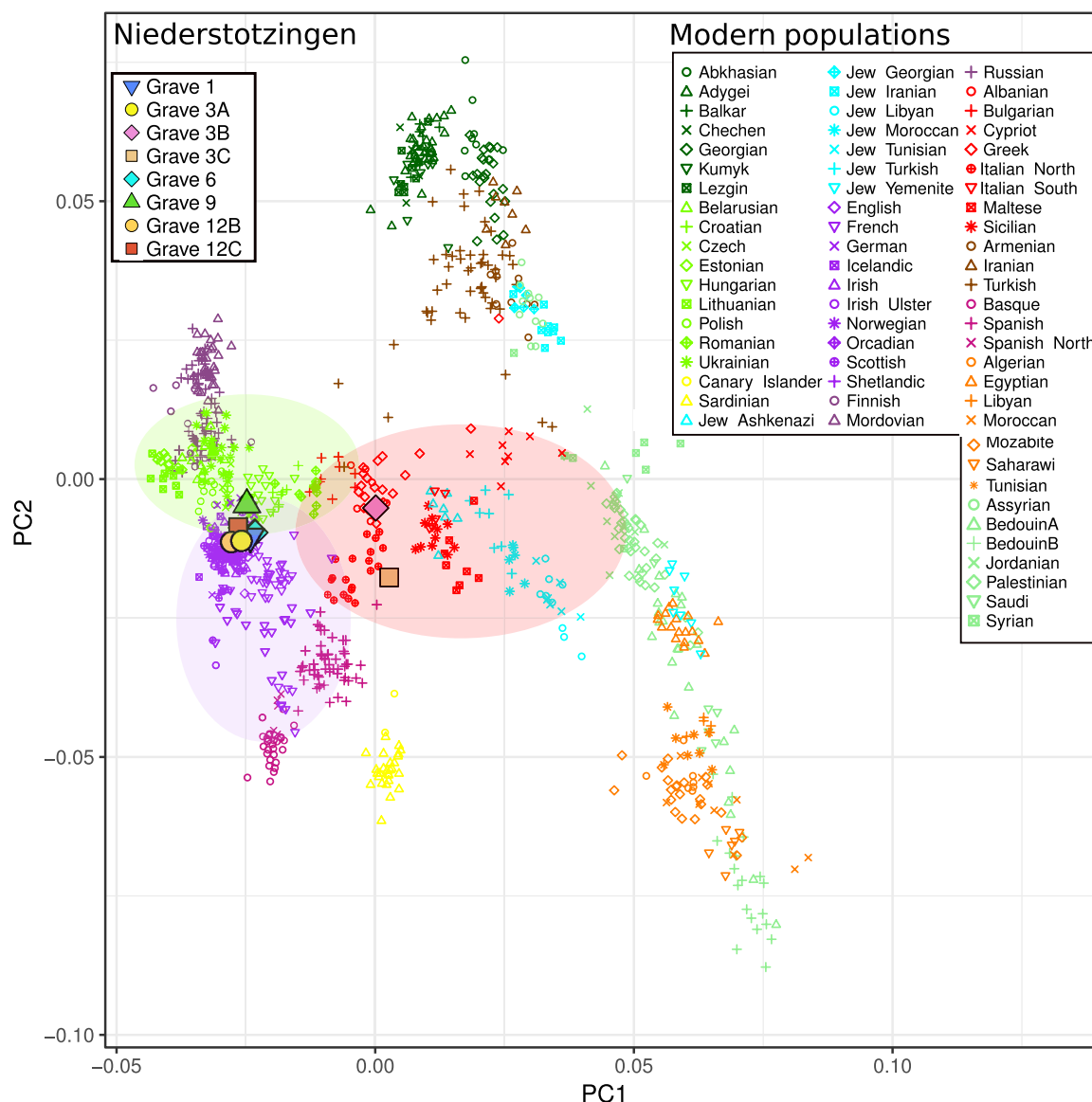


Fig. 2. PCA plot of Niederstotzingen individuals, modern west Eurasians, and selected ancient Europeans. Genome-wide ancient data were projected against modern west Eurasian populations. Colors on PCA indicate more general Eurasian geographic boundaries than countries: dark green, Caucasus; bright green, eastern Europe; yellow, Sardinia and Canary Islands; bright blue, Jewish diaspora; bright purple, western and central Europe; red, southern Europe; dark brown, west Asia; light purple, Spain; dark purple, Russia; pale green, Middle East; orange, North Africa. The transparent circles serve to highlight the genetic overlap between regions of interest.

direct evidence for incoming mobility at the site and for contact that went beyond exchange of grave goods (4). *Familia* had holdings across the Merovingian Kingdom and traveled long distances to maintain them; these holdings could have extended from northern Italy to the North Sea. Nobles displayed and accrued power by recruiting outside individuals into the household as part of their traveling retinue. Extravagant burial rites of these *familia* are symbolic evidence of the Frankish power systems based on people *Personenverbandstaaten* imposed from the 5th until the 8th century CE (4). The assignment of grave goods and the burial pattern do not follow any apparent pattern with respect to genetic origin or provenance, suggesting that relatedness and fellowship were held in equal regard at this burial.

Further insights into the kinship structure are obtained from the reconstruction of direct relatives at the site. We demonstrated that five of the individuals (1, 3A, 6, 9, and 12B) were kin to at least second degree (Fig. 3 and tables S15 and S16); four of these were buried with distinguishable grave goods (discussed above and in fig. S1). These data show that at Niederstotzingen, at least in death, diverse cultural affiliations could be appropriated even within the same family across just two generations. This finding is somewhat similar to the burial of the Frankish King Childeric in the 5th century CE with a combination of Frankish and Byzantine grave goods that symbolized both his provenance and military service to the Romans (4). The burial of three unrelated individuals (3B, 3C, and 12C) in multiple graves beside the rest of the cohort would imply that this Alemannic group buried their dead based on a combination of familial ties and fellowship. One explanation could be that they were adopted as children from another region to be trained as warriors, which was a common practice at the time; these children were raised with equal regard in the *familia* (2, 4).

To infer a tentative family tree, we combined autosomal SNPs, NRY haplotypes, mtDNA haplotypes, and age-at-death data. It is possible that pairs 9/1, 9/3A, and 1/6 represent father-son relationships. The results also support that pairs 1/3A and 9/12B are siblings, as they share the same maternal haplotype (K1a and X2B4, respectively). Pairs 3A/6, 1/12B, 6/9, and 3A/12B are second degree-related, that is, they resemble uncles/cousins to sibling pair 1/3A. An infant buried in grave 4 has the same mtDNA haplotype (X2b4) as 9 and 12B, which supports a maternal relation, but there is no further genomic information to confirm this possibility. This family tree is based on the assumption that the individuals died over a relatively short time period. However, archeological evidence suggests that the gravesite may have been used for two generations (circa 580 to 630 CE) (8), which allows the possibility of multiple scenarios when constructing a family tree. Notably, individual 9, who is buried with Frankish grave goods (8), might have represented the highest-ranking individual and head of the household, given his close kinship to the four others and prominence in the burial rites.

The 7th century CE burial in Niederstotzingen represents the best-preserved example of an Alemannic *Adelsgrablege*. The observation that burial of the remains was close to a Roman crossroads, orientated in a considered way, and associated with rich grave goods points to a noble gravesite of an Alemannic *familia* with external cultural influences. The high percentage of males in the burial site suggests that this site was intended for a ranked warrior group, meaning that the individuals are not representative of the population existing in 7th century CE Alemannia. The kinship estimates show that kinship structure was organized around the *familia*, which is defined by close association of related and unrelated individuals

united for a common purpose. The apparent kinship structure is consistent with the hypothesized *Personenverbandstaaten*, which was a system by which Merovingian nobles enforced rule in the Duchies of Alemannia, Thuringia, Burgundy, and elsewhere. Beyond the origin of the grave goods, we show isotopic and genetic evidence for contact with communities external to the region and evidence for shared ancestry between northern and southern Europeans. This finding invites debate on the Alemannic power system that may have been highly influenced by mobility and personal relations.

MATERIALS AND METHODS

Molecular analysis

Teeth were sampled from all 13 individuals previously excavated at Niederstotzingen (Fig. 1 and table S1) (6). aDNA was isolated from dentine with the protocol of Rohland *et al.* (31). Double-stranded libraries were prepared for sequencing (32, 33), and some libraries were treated with UDG (table S5) (34). To enrich the endogenous content of libraries, mtDNA (35) and autosomal DNA (36) (probe set of 1.24 million autosomal SNPs, hereafter referred to as 1240K) were captured using in-solution probes (17). Libraries were sequenced on Illumina HiSeq 2500, NextSeq, and Illumina HiSeq 4000 platforms using 75–base pair paired-end sequencing kits.

Data analysis

To process raw sequences, default parameters of EAGER (37) were applied. Sequences were mapped to human genome (build Hg19) (38, 39) and the mtDNA reference (rCRS) (40). The minimum mapping and base quality were both 30. MapDamage2.0 quantified deamination at 5' and 3' ends in non-UDG-treated libraries to show the presence of aDNA (41). To authenticate the retrieved data, mtDNA and X chromosome contamination estimates were made with Schmutzi (42) and ANGSD (43), respectively. To investigate the impact that modern contamination may have had on the results, non-UDG-treated data (shotgun and mtcapture) were filtered with PMDtools (threshold 3) and analyzed in parallel with non-PMD-filtered reads (22).

To retrieve mtDNA haplotypes, stringent filtering with log2fasta (42) was applied (quality > 20) to create mitogenome sequences. mtDNA haplotypes were assigned with haplofind (phylotree 17) (44, 45). The NRY haplotypes were identified relative to ISOGG database 11.349 (<https://isogg.org/tree>), and haplotyping was performed with ANGSD haploid caller (43) guided by yhaplo tool (46). Low-coverage (<2X) Y SNPs that were potentially caused by deamination were filtered. To estimate the sex of the individuals, the relative coverage of X and Y chromosomes was calculated from shotgun (23, 47) and 1240K capture (24) sequences.

To investigate genomic data, SAMtools mpileup (38) and PileupCaller (<https://github.com/stschiff/sequenceTools/tree/master/src-pileupCaller>) called pseudodiploid genotypes for the individuals, at loci that overlapped with the 1240K targeted SNPs, and merged them to a Human Origins Affymetrix (25) modern west Eurasian subset ($n = 1063$) (26). PCA smartpca (48, 49), admixture (50), and outgroup F3 statistics made estimates of ancestry from genome-wide data (25, 26). Admixture was run from 2 to 12 components (K), cross-validation (--cv) with five replications each, and random seeding (-s 1-1000). The selection of the admixture results to present was based on the lowest CV error, the replicate with the highest log likelihood, and careful interpretation of the results (51). Kinship estimates used the READ tool and the coefficient of relatedness, which were adapted for low-coverage genotypes (16, 27).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/4/9/eaao1262/DC1>

Supplementary Materials and methods

Fig. S1. Photographs of burial goods with most specific cultural identifying markers.

Fig. S2. Isotope $^{86}\text{Sr}/^{87}\text{Sr}$ and $\delta^{18}\text{O}$ values for enamel from teeth.

Fig. S3. Overlaying shotgun and mtDNA deamination plots from mapDamage quantification against the reference genome.

Fig. S4. Genetic sex estimates from genome-wide capture.

Fig. S5. Admixture estimates for west Eurasians, Niederstotzingen, and selected ancient individuals.

Fig. S6. F3 outgroup statistics for Niederstotzingen 1 using Mbuti as an outgroup.

Fig. S7. F3 outgroup statistics for Niederstotzingen 3A using Mbuti as an outgroup.

Fig. S8. F3 outgroup statistics for Niederstotzingen 3B using Mbuti as an outgroup.

Fig. S9. F3 outgroup statistics for Niederstotzingen 3C using Mbuti as an outgroup.

Fig. S10. F3 outgroup statistics for Niederstotzingen 6 using Mbuti as an outgroup.

Fig. S11. F3 outgroup statistics for Niederstotzingen 9 using Mbuti as an outgroup.

Fig. S12. F3 outgroup statistics for Niederstotzingen 12B using Mbuti as an outgroup.

Fig. S13. F3 outgroup statistics for Niederstotzingen 12C using Mbuti as an outgroup.

Table S1. PCR-based haplotyping of DNA extracts from previous study.

Table S2. Archeological context and isotopes.

Table S3. Shotgun sequencing output and mapping data.

Table S4. mtDNA capture sequencing output data and mapping.

Table S5. 1240K sequencing output data and mapping.

Table S6. Schmutzi estimation of mtDNA contamination.

Table S7. ANGSD X chromosome contamination estimate on 1240K libraries.

Table S8. Haplogroups and private mutations for each mtDNA capture (phylotree 17).

Table S9. Complete list of NRY haplogroups with identifying ISOGG markers for 1240K capture sequences.

Table S10. Sex estimates from shotgun and genome-wide capture data.

Table S11. Sex estimates from shotgun data based on Rx values.

Table S12. Admixture CV error values for each component and individual.

Table S13. Shotgun reads with PMDtools threshold 3 filtered and skoglund sex estimate of filtered reads.

Table S14. Haplogroup calling of selected individuals before and after PMD (threshold 3) filtering.

Table S15. READ pairwise kinship-based estimate.

Table S16. Pairwise estimate of kinship and coefficient of relatedness.

References (52–58)

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